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Plant N capture from pulses: effects of pulse size, growth rate, and other soil resources

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Abstract In arid ecosystems, the ability to rapidly capture nitrogen (N) from brief pulses is expected to influence plant growth, survival, and competitive ability. Theory and data suggest that N capture from pulses should depend on plant growth rate and availability of other limiting resources. Theory also predicts trade-offs in plant stress tolerance and ability to capture N from different size pulses. We injected $K^{15}NO_3$, to simulate small and large N pulses at three different times during the growing season into soil around the co-dominant Great Basin species *Sarcobatus vermiculatus*, *Chrysothamnus nauseosus* ssp. *consimilis*, and *Distichlis spicata*. Soils were amended with water and P in a partial factorial design. As predicted, all study species showed a comparable decline in N capture from large pulses through the season as growth rates slowed. Surprisingly, however, water and P availability differentially influenced the ability of these species to capture N from pulses. *Distichlis* N capture increased up to tenfold with water addition while *Chrysothamnus* N capture increased up to threefold with P addition. *Sarcobatus* N capture was not affected by water or P availability. Opposite to our prediction, *Sarcobatus*, the most stress tolerant species, captured less N from small pulses but more N from large pulses relative to the other species. These observations suggest that variation in N pulse timing and size can interact with variable soil water and P supply to determine how N is partitioned among co-existing Great Basin species.

Keywords Arid ecosystems · Great Basin desert · Nitrogen isotopes · Plant N demand · Soil resource pulses

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Introduction

In arid and semiarid ecosystems, water and nitrogen (N) limit growth and are mainly available to plants in brief pulses following precipitation events (Noy-Meir 1973). Water input following prolonged dry periods stimulates N mineralization (Fisher et al. 1987; Austin et al. 2004) and facilitates N movement to roots (Nye and Tinker 1977). For example, in the Great Basin and Mojave desert simulated and natural precipitation events following drought can increase soil inorganic N concentrations threefold to tenfold (Cui and Caldwell 1997a; Z. Aanderud unpublished data). These N pulses, however, are brief, with plant and microbial N uptake lowering available N to pre-pulse levels within days (Cui and Caldwell 1997a; Hodge et al. 1999).

While the temporal dynamics of N in arid systems long have been recognized, only relatively recently have there been attempts to understand how such temporal heterogeneity affects ecological processes. Although current theory predicts that pulsed resource supply should affect productivity, resource partitioning, and species interactions (Goldberg and Novoplansky 1997; Chesson et al. 2001; Chesson et al. 2004), experimental manipulation of N pulses in arid systems have produced disparate results. In some studies, pulsed N increased plant growth, facilitated N partitioning among species, or altered competitive ability (Bilbrough and Caldwell 1997; Cui and Caldwell 1997b; Gebauer and Ehleringer 2000). In a number of other studies, however, N pulses have influenced these processes little (Gebauer et al. 2002; Yoder and Caldwell 2002; Ivans et al. 2003).

Improved understanding of the mechanisms regulating plant response to N pulses may provide insight into these conflicting results, allowing more accurate prediction of the effects of pulsed N supply on these ecological processes.

Optimal foraging models predict and experimental data demonstrate that plants modify physiological and morphological responses to variable resource supply so resource uptake will match plant growth requirements (Drew and Saker 1975; Bloom et al. 1985; Gleeson and Tilman 1992; Gleeson and Good 2003). As a result, N uptake during pulses should not necessarily vary directly with soil N concentration, but should instead largely depend on plant N demand (Forde 2002; Collier et al. 2003). Plant N demand can be operationally defined as the minimum amount of N needed for maximum growth during a specified growth stage under a given set of environmental conditions; thus, plant N demand is a function of relative growth rate (RGR) and tissue N status (Jeuffroy et al. 2002). Seasonal declines in growth rate associated with phenology, therefore, decrease N demand and likely reduce plant N capture from pulses (Eissenstat and Caldwell 1988; Larigauderie and Richards 1994; Bilbrough and Caldwell 1997).

Low soil water and phosphorus (P) availability in arid systems also can lower N demand by decreasing growth rate or by reducing plant carbohydrate or P status relative to N (Foyer et al. 1998; Stitt 1999; Drenovsky and Richards 2004). In addition to direct effects on plant N demand, both drought stress and low soil P can inhibit root N uptake capacity (Schjorring 1986; Matzner and Richards 1996; Kim et al. 2003). While temporal variation in water input is substantial in the Great Basin (Smith et al. 1997) and soil P availability can vary more than threefold both within the horizontal rooting distribution of an individual plant and at larger spatial scales across the community (Jackson and Caldwell 1993; Donovan and Richards 2000), differences in water and P availability may not affect N capture equally in all species. Some desert grasses and shrubs can restore N uptake capacity within days following rewatering, while uptake capacity in other species remains inhibited (BassiriRad and Caldwell 1992; BassiriRad et al. 1999). Likewise, some desert species can forage for or recycle P very efficiently so that plant P status remains sufficient despite low soil P (Jackson and Caldwell 1989; Drenovsky 2002). In these species, low soil P availability may not affect plant N demand or root N uptake capacity.

Species also may differ in relative abilities to capture N from different size pulses. Glasshouse experiments with grasses suggest less stress tolerant species may have a greater ability to capture N from large pulses through rapid growth of relatively short-lived roots, while species that maintain an active root system under stressful soil conditions may have a greater ability to acquire N from smaller or more transient pulses (Grime 1994). Although N pulse size is known to vary with the frequency and magnitude of precipitation events in arid systems (Noy-Meir 1973), no field studies, which we are aware of, have determined if there is a trade-off between stress tolerance and ability to respond to N pulses of different sizes.

In the Great Basin, species are adapted to maximize growth during the spring, as soil and air temperatures warm and snow melt and spring rains have recharged soil moisture (Comstock and Ehleringer 1992). In our model system, the three co-dominant species, *Sarcobatus vermiculatus* (Hook.) Torrey (C_3 shrub), *Chrysothamnus nauseosus* (Palla.) Britt. ssp. *consimilis* (E. Greene) H.M. Hall and Clements (C_3 shrub) and *Distichlis spicata* (L.) E. Greene (C_4 grass) leaf out in early spring, have highest growth rates in midspring, and flower and set seed in late summer. Although seasonal changes in growth rate likely will influence N capture from pulses, given their similar phenology, other factors such as limited water and P availability and N pulse size are potentially more important in determining how N is partitioned among these dominant species.

We determined the extent that seasonal changes in growth rate and low soil water and P availability regulates the magnitude of whole-plant N capture from pulses and partitioning of N within our Great Basin system. We also evaluated if the three co-existing species, known to differ in stress tolerance, differ in ability to respond to N pulses of different size. For all study species, we predicted that N capture from large experimental N pulses would be greatest when pulses occurred in early spring and would decline seasonally as growth rates slowed. However, when water and P availability was increased, we predicted that all species would capture more N relative to control plants, regardless of when the pulse occurred in the season. We also predicted that *Sarcobatus*, the species most tolerant to drought and low nutrient availability, would capture more N from small N pulses than *Chrysothamnus* and *Distichlis*, while the opposite would be observed under large N pulses.

Methods

Study area and species

This research was conducted at the Mono Basin Ecosystem Research Site (MBERS), California, USA, located at the western edge of the Great Basin biogeographic province (38°5′N, 118°58′W; 1,958-m elevation). Climate at the site is arid with a mean annual precipitation of 160 mm with more than 80% of the snow and rain arriving between October and May (Snyder et al. 2004). Average soil pH in the 0–15 cm layer is 9.6, saturated paste electrical conductivity is 3.8 dS m^{-1}, Olsen's soil-extractable P is 2.8 mg kg^{-1} and total soil N is 0.3 g kg^{-1} (Donovan and Richards 2000; Drenovsky and Richards 2004). The three co-dominant study species, *Chrysothamnus*, *Sarcobatus*, and *Distichlis*, constitute over 95% of the perennial plant cover. Rooting density of the shrubs, *Chrysothamnus* and *Sarcobatus*, is

highest in the upper 50 cm of soil and roots of both species reach the capillary fringe of ground water at the site (3–5 m). Although roots of the rhizomatous grass, *Distichlis*, form extensive dense mats in the upper 30 cm of soil, *Distichlis* roots only extend to a depth of 2–3 m at this site (J. Richards, unpublished data). *Sarcobatus* readily colonizes nutrient poor, alkaline–saline soils, and is substantially more drought tolerant than *Chrysothamnus*. *Sarcobatus* midday water potentials (−2.1 to −4.0 MPa) are more than twofold lower throughout the growing season than co-occurring *Chrysothamnus*, and a high magnitude of hydraulic lift by *Sarcobatus* allows it to maintain active roots in soils with water potentials at least as low as −3 MPa (Donovan et al. 1996, 2003). While comparative water relations and nutrient data are lacking for *Distichlis* at this site, experiments in the southern Great Basin suggest *Distichlis* stress tolerance is intermediate between the two shrubs (J. Richards, unpublished data).

Experimental design and N pulse application

Five blocks were selected in winter 2002, each containing 60, 1 m^2 quadrats. Within each block, 15 quadrats contained *Chrysothamnus* shrubs, 15 quadrats contained *Sarcobatus* shrubs, and 30 quadrats contained *Distichlis* tillers. Quadrats with similar shrub size and density (canopy dimensions c. 20×20×35 cm; 1 shrub m^{-2}) and grass cover (2 g m^{-2}) were selected in each block. All experimental quadrats were at least 3-m apart.

Nitrogen was applied as either a small (28 mg N m^{-2}) or large (5 g N m^{-2}) pulse three times during the growing season (April 11, May 3, or June 1) by injecting $K^{15}NO_3$ (99 and 1 atom % ^{15}N, respectively, for the small and large N pulses) evenly through the 0–30 cm soil layer in 64 injection sites per quadrat. The injection sites were spaced evenly over the 1 m^2 quadrat using a 10×10-cm grid pattern. A syringe and needle were used to inject 10 ml of solution at each injection site. The needle was inserted 30 cm into the soil and slowly pulled up through the soil profile as the ^{15}N solution dispersed horizontally through four holes drilled around the sealed tip. Nitrate was chosen as the label because it is the predominant form of available N in the system and because ammonium would volatilize at the high soil pH (Vega-Jarquin et al. 2003). By applying a small amount of highly enriched N in our small pulse, we were able to trace plant NO_3^- capture without significantly increasing the size of the soil inorganic N pool (c. 4 mg kg^{-1} in early spring, see Results). Our large N pulse, however, was expected to increase soil inorganic N to c.14 mg kg^{-1} (based on spring soil inorganic N concentrations, mass of N injected in the 1 m^2 quadrats to a depth of 30 cm, and soil bulk density). Previous studies in the Great Basin have demonstrated that moderate water inputs can produce N pulses ranging from 5 mg kg^{-1} to 15 mg kg^{-1} (Cui and Caldwell 1997a; Ivans et al. 2003; Peek and Forseth 2003). Our small and large N pulses, therefore, are comparable to the range in which N pulse size can vary naturally.

Water and P were applied prior to the small and large N pulses in a partial factorial design. Before small N pulses were applied, plants received either: no water or P (control), only water (W), or water and P (W + P). These three treatments allowed us to evaluate if water and P limitations can affect N capture from pulses. Before large N pulses were applied plants received either: water (W) or water and P (W + P). These two treatments allowed us to evaluate the effect of seasonal declines in plant growth rate on N capture without the confounding effects of seasonal declines in soil water, N, or P availability. Water was spread evenly over the quadrat as a simulated 20-mm rain event 2 days before ^{15}N injection. P was added at a rate of 18 g P m^{-2} (as NaH_2PO_4 salt) in late winter 2002, before new root and shoot growth occurred and soils were moist, by trenching two, 15-cm deep rows across the quadrat, mixing the P with the excavated soil and back-filling the trenches. Different plants were used for each of the 15 treatment combinations. Each treatment combination was replicated once in each block for *Chrysothamnus* and *Sarcobatus* and twice in each block for *Distichlis*.

Relative growth rates

For each species, the aboveground biomass of 15 replicate, nonexperimental plants was harvested at four times: immediately before the April, May, and June N pulses and 20 days following the June N pulse. For these measurements, shrubs were selected to match the size of the experimental plants and for *Distichlis*, 1 m^2 quadrats were selected with cover similar to quadrats used for experimental N pulses. Relative growth rates (RGR) was calculated as: $RGR = [\ln(M_f) - \ln(M_i)]/(t_f - t_i)$ where M_f and M_i are aboveground biomass harvested at the beginning (M_i) and end (M_f) of each growth interval.

Plant ^{15}N capture, leaf nutrient status, and soil N pools

We estimated ^{15}N capture of the study species by harvesting the above ground biomass in each quadrat 20 days following label application and quantifying changes in shoot ^{15}N pools using a ^{15}N mass balance equation (Nadelhoffer and Fry 1994). It was not possible to separate roots by species in the field, so our measure of species ^{15}N capture does not include ^{15}N capture and storage in roots. We did, however, estimate ^{15}N capture by roots on a community basis. Roots were sampled by hammering 4 cores (5.1 cm dia × 30 cm dia) into each quadrat and sifting the sandy soil through a 1-mm screen. All tissue samples were triple rinsed with deionized water, oven-dried at 65°C to a constant mass and then finely ground. Tissue N concentration and ^{15}N enrichment were measured by continuous flow direct

combustion and mass spectrometry at the University of California Davis Stable Isotope Facility. Samples for P analysis were microwave digested with nitric acid and analyzed by ICP-AES (Thermo Jarrell Ash Corp., Franklin, MA, USA) (Sah and Miller 1992).

Total ^{15}N recovery in the plant community and changes in soil N pools 20 days after each N pulse were determined by pooling the shoot and root data from the three species quadrats within each treatment within each block because roots could not be separated by species in the field. A subset of the five resource amendment treatments was analyzed: small N pulse, small N pulse + water and large N pulse + water. ^{15}N recovery in shoots, roots, and total vegetation was calculated as the mass of ^{15}N recovered/mass of ^{15}N applied. Extractable NH_4^+, NO_3^- and dissolved organic N (DON) were quantified on root-free soils from the four sifted soil cores. The cores were composited for each replicate and then a 60-g subsample was extracted with 0.1 M K_2SO_4. Extractable NO_3^- and NH_4^+ and total dissolved nitrogen (TDN) were measured following Forster (1995) for NH_4^+, Miranda et al. (2001) for NO_3^- and Cabrera and Beare (1993) for TDN. DON was estimated as [TDN–($NO_3^- + NH_4^+$)].

Statistical analyses

Effects of species, pulse timing, and treatment on ^{15}N capture were analyzed separately for the small and large N pulses by ANOVA. Assumptions of ANOVA were evaluated using the Shapiro–Wilk test for normality and Levene's test for homogeneity of variance. When these assumptions were violated, data were weighted by the inverse of the variance (Neter et al. 1990). Factor effects were evaluated using Type III sums of squares. Following ANOVA, linear contrasts were used to analyze a priori comparisons of species ^{15}N capture. Similarly, effects of pulse timing and treatment on ^{15}N recovery in the vegetation and soil N pools were analyzed with ANOVA followed by contrasts. Data were analyzed with SAS (SAS-Institute 2001).

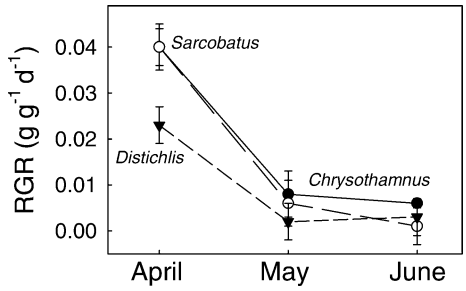

Fig. 1 Relative growth rates (*RGR*) for the three study species during the 2002 growing season (mean ± SE, $n = 15$ for each time period for each species). Measurements were made by harvesting matched sets of naturally established, nonexperimental plants, and quantifying leaf and stem biomass four times during the 2002 growing season: April 11, May 3, June 1, and June 22. The April RGR value corresponds to the growth April 11–May 3 interval, the May value corresponds to the May 3–June 1 interval, and the June value corresponds to the June 1–June 22 interval

Results

RGR and species ^{15}N capture

Relative growth rates for all study species was highest during the April pulse and declined sharply through the May and June pulses (Fig. 1). The two shrubs had similar RGR throughout the growing season, while the grass, *Distichlis*, had a slightly lower RGR than the shrubs during April.

The three-way interaction (pulse timing × treatment × species) for shoot ^{15}N content was significant for both the small and large N pulses, indicating that for both pulse sizes, differences in ^{15}N capture between species were due to the timing of the N pulse and the availability of other soil resources (Table 1). Under ambient soil resource conditions (control), ^{15}N capture from small N pulses declined in all species through the season ($P < 0.01$, Fig. 2). For both shrubs, a significant seasonal decline in ^{15}N capture from small N pulses occurred even when soil water availability was increased prior to the pulse ($P < 0.05$). The absolute amount of

Table 1 ANOVA results (df, *F*, and *P*) for shoot ^{15}N content (mg ^{15}N m^{-2})

Source	N pulse size					
	Small N pulse			Large N pulse		
	df	*F*	*P*	df	*F*	*P*
Block	4	1.45	0.2208	4	0.65	0.6271
Pulse timing	2	8.29	0.0004	2	6.79	0.0018
Treatment	2	2.72	0.0693	1	0.71	0.420
Species	2	31.91	< 0.0001	2	25.43	< 0.0001
Pulse timing × treatment	4	8.28	< 0.0001	2	0.82	0.4451
Pulse timing × species	4	4.32	0.0025	4	1.94	0.1110
Pulse timing × treatment × species	12	5.65	< 0.0001	6	3.24	0.0062
Error	142			93		

The three independent factors, pulse timing (April, May, and June), treatment (control, water, and water + P for the low N pulse and water and water + P for the large N pulse), and species (Chrysothamnus, Distichlis, and Sarcobatus), and their interactions were analyzed separately for the small (28 mg N m^{-2}) and large (5 g N m^{-2}) N pulses. Data are presented in Fig. 2

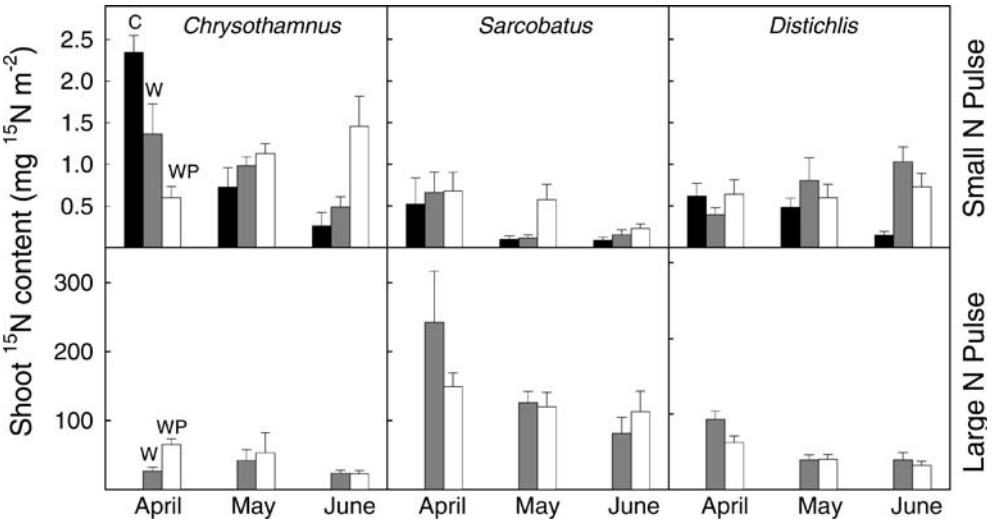

Fig. 2 Shoot ^{15}N content of the study species 20 days after an April, May, or June N pulse (mean ± SE, $n = 5$–10). Before the small N pulse (28 mg N m^{-2}) was applied, soils received no amendments (*C*), a simulated 20-mm rain event (*W*), or a simulated 20-mm rain event and 18 g P m^{-2} (*WP*). For plants receiving the large N pulse (5 g N m^{-2}) soils were amended with either a simulated 20-mm rain event (W) or a 20 mm rain event and 18 g P m^{-2} (*WP*). Note, the difference in scale for the *y*-axis between the small and large N pulse graphs

^{15}N capture by shrubs from small N pulses did not differ between control and water treatments following any of the pulses ($P > 0.05$). In contrast, *Distichlis* ^{15}N capture from small N pulses increased seasonally with improved soil water availability ($P = 0.001$). With both water and P addition, *Chrysothamnus* ^{15}N capture from small N pulses increased significantly through the season compared to plants receiving only water ($P = 0.03$), but P addition did not alter the pattern of seasonal N capture of *Sarcobatus* and *Distichlis* relative to plants only receiving water ($P > 0.05$).

Sarcobatus and *Distichlis* ^{15}N capture from large N pulses following water addition declined significantly through the season ($P = 0.043$ and $P = 0.004$, respectively; Fig. 2) and was not influenced by P addition ($P > 0.05$). In contrast, *Chrysothamnus* ^{15}N capture from large pulses increased twofold following the April pulse with P addition relative to plants only receiving water. As a result, only with P addition was there a significant seasonal decline in *Chrysothamnus* ^{15}N capture from large pulses ($P = 0.003$).

Leaf N and P concentrations

Leaf N and P did not increase with water addition followed by a small N pulse in any of the species ($P > 0.05$). Averaged across the three large N pulses, *Sarcobatus* leaf N increased 58% relative to plants receiving water and a small N pulse, with the largest increase occurring during the April pulse (Fig. 3). Averaged across the three large N pulses *Distichlis* leaf N increased 21% with the largest increases occurring later in the growing season. In contrast, *Chrysothamnus* leaf N following large N pulses increased less than 10% across the three pulses and was only significantly greater than plants receiving water during the May pulse ($P = 0.043$). However, P addition increased *Chrysothamnus* leaf P, but not *Sarcobatus* or *Distichlis*

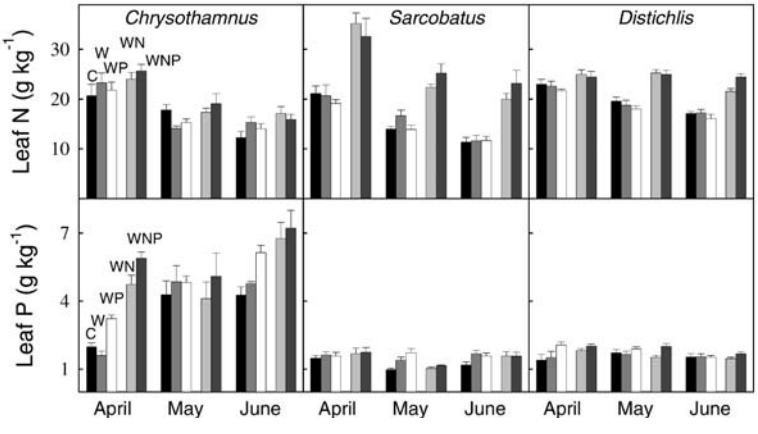

Fig. 3 Leaf N and P concentrations of the study species 20 days after an April, May, or June N pulse (mean ± SE, $n = 5$–10). Treatments included no soil amendments (*C*), a simulated 20-mm rain event only (*W*), a simulated 20-mm rain event and 18 g P m^{-2} (*WP*), a simulated 20-mm rain event and 5 g N m^{-2} (*WN*), and a simulated 20-mm rain event plus 5 g N m^{-2} and 18 g P m^{-2} (*WNP*). The small N pulse (28 mg N m^{-2}) applied to the C, W and W + P treatments was not expected to produce a fertilizer effect

leaf P relative to plants only receiving water. Greater soil N availability also increased *Chrysothamnus* leaf P. In April and June, *Chrysothamnus* leaf P was 3- and 1.5-fold greater in plants receiving water and a large N pulse than in plants receiving only water and a small N pulse. These nutrient interactions were not observed in the other species.

Plant community ^{15}N recovery and soil N pools

On a plant community basis (shoots + roots) ^{15}N capture from small pulses declined through the season under ambient soil conditions ($P = 0.034$; Table 2), but increased with water addition ($P = 0.043$). These different seasonal patterns of ^{15}N capture were mainly due to increased root ^{15}N content when soil water availability was increased. In contrast,^{15}N capture from large N pulses declined significantly through the season ($P = 0.003$), due to decreases in both shoot and root ^{15}N content.

Recovery of ^{15}N in the plant community 20 days following a small N pulse was substantial (Table 2). Averaged across the April, May, and June pulses, more than 60% of the ^{15}N applied was recovered in the plant community (shoots + roots) in quadrats not receiving water. With water addition prior to a small pulse, recovery of ^{15}N in the plant community averaged more than 65%. In contrast, ^{15}N recovery in the plant community from large N pulses with water addition averaged less than 10% across the April, May, and June pulses.

Prior to the application of the first experimental N pulse, soil NH_4^+, NO_3^- and DON concentrations were 0.31 ± 0.1, 4.15 ± 0.6, 1.01 ± 0.1 mg kg^{-1} (mean ± SE, $n = 8$), respectively. Soil NH_4^+ levels 20 days following a pulse were very low and not affected by pulse timing, water addition, or pulse size (Table 3). Soil NO_3^- levels were similar and low in both control and watered soils 20 days following small N pulses regardless of pulse timing, but were significantly higher in soils 20 days after a large N pulse ($P < 0.05$). DON levels remained low through the season and were not affected by pulse timing ($P > 0.05$) but increased following large N pulses ($P < 0.05$).

Discussion

To quantify the effects of growth rate on N demand and N capture, it was necessary to minimize the effect of low N supply rates on N capture. In this experiment, we

Table 2 Temporal patterns of ^{15}N capture and allocation to shoots, roots, and total vegetation (shoots + roots) and ^{15}N recovery 20 days following April, May, and June N pulses

Month	Plant component	^{15}N pool (mg m^{-2})			^{15}N recovery (%)		
		Small N pulse	Small N pulse + water	Large N pulse + water	Small N pulse	Small N pulse + water	Large N pulse + water
April	Shoot	2.2 ± 0.5	1.3 ± 0.1	189.0 ± 28.1	8.0 ± 1.6	4.7 ± 0.4	3.8 ± 0.6
	Root	17.3 ± 2.7	13.7 ± 2.2	606.1 ± 140.5	61.9 ± 9.8	48.9 ± 7.7	12.1 ± 2.8
	Vegetation	19.6 ± 2.9	15.1 ± 2.1	795.1 ± 142.4	69.9 ± 10.3	53.8 ± 7.6	15.9 ± 2.8
May	Shoot	0.8 ± 0.1	1.4 ± 0.1	119.3 ± 12.6	3.0 ± 0.4	5.1 ± 0.5	2.4 ± 0.2
	Root	16.1 ± 1.7	19.7 ± 1.6	199.4 ± 22.9	57.5 ± 6.2	70.4 ± 5.6	4.0 ± 0.5
	Vegetation	16.9 ± 1.8	21.1 ± 1.6	324.3 ± 27.9	60.5 ± 6.4	75.4 ± 5.7	6.5 ± 0.6
June	Shoot	0.3 ± 0.1	1.46 ± 0.1	95.9 ± 12.8	1.0 ± 0.3	5.2 ± 0.5	1.9 ± 0.3
	Root	13.5 ± 1.8	18.9 ± 1.6	261.1 ± 32.5	48.3 ± 6.6	67.7 ± 5.6	5.2 ± 0.6
	Vegetation	13.8 ± 1.9	20.4 ± 1.6	356.9 ± 35.1	49.3 ± 6.8	72.9 ± 5.8	7.1 ± 0.7

A subset of the five treatments was quantified: a small ^{15}N pulse (28 mg N m^{-2}) applied to nonamended (control) soils, a small ^{15}N pulse following a 20-mm rain event, and a large ^{15}N pulse (5 g N m^{-2}) following a 20-mm rain event (mean ± SE, $n = 20$). Data were pooled across quadrats containing the three study species for each treatment in each block. ^{15}N recovery was calculated as the mass of ^{15}N in the vegetation components 20 days after the pulse was applied divided by the mass of ^{15}N applied

Table 3 Temporal patterns of N concentration in soil N pools (mg kg^{-1}) 20 days after April, May, and June N pulses

A subset of the five treatments was quantified: a small ^{15}N pulse (28 mg N m^{-2}) applied to nonamended (control) soils, a small ^{15}N pulse following a 20-m rain event, and a large ^{15}N pulse (5 g N m^{-2}) following a 20-mm rain event (mean ± SE, $n = 10$)

Pulse	Soil pool	N concentration		
		Small N pulse	Small N pulse + water	Large N pulse + water
April	NH_4^+	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
	NO_3^-	2.4 ± 0.3	0.8 ± 0.1	5.5 ± 0.1
	DON	0.9 ± 0.4	1.1 ± 0.2	2.6 ± 0.1
May	NH_4^+	0.3 ± 0.1	0.1 ± 0.1	0.3 ± 0.1
	NO_3^-	2.1 ± 0.5	0.9 ± 0.1	5.8 ± 0.2
	DON	0.9 ± 0.1	1.3 ± 0.2	2.0 ± 0.1
June	NH_4^+	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
	NO_3^-	0.6 ± 0.2	1.0 ± 0.2	4.2 ± 0.1
	DON	1.6 ± 0.2	0.9 ± 0.2	2.3 ± 0.1

quantified the effects of growth rate on N capture by calculating the proportional decline in plant N capture from early season pulses when growth rates were high to late season N pulses when growth rates were low (Fig. 1), under conditions of high soil N supply (i.e., large N pulse with water, Fig. 2, lower panels). Under these conditions, N capture from large pulses declined 46 and 33% through the growing season for *Sarcobatus* and *Distichlis*, respectively (Fig. 2, lower panels). However, *Chrysothamnus* N capture from large pulses remained relatively constant, and low, through the growing season despite large changes in growth rates. Only when P supply was increased did *Chrysothamnus* N capture from large pulses decline seasonally with growth rate. Under these conditions, *Chrysothamnus* N capture declined 41% through the season (Fig. 2, lower panel). Nevertheless, seasonal declines in N capture from large pulses were apparent in our community level measurements that included root ^{15}N capture, with ^{15}N capture by the vegetation declining 45% through the season (Table 2). These seasonal declines in N capture from relatively large N pulses are comparable to values reported for other cold desert shrubs and grasses (Bilbrough and Caldwell 1997). Thus, our prediction that N capture from large N pulses would be greatest in early spring when growth rates were high and decline seasonally as growth rates slowed, was partially supported. The large seasonal decreases in N capture from large pulses by *Sarcobatus* and *Distichlis* suggest that seasonal declines in N demand as a function of growth rate can reduce N capture from pulses. For *Chrysothamnus*, however, it appears that N demand is mainly driven by P availability rather than changes in growth rate through the season; only when P supply was sufficient did seasonal declines in growth rate reduce N capture from large pulses.

Most studies documenting large temporal differences in plant N uptake between species have been conducted in old fields and grassland systems (Fitter 1986; McKane et al. 1990; Mamolos and Veresoglou 2000). In contrast to those systems, our study and previous literature reports provide little evidence to suggest perennial Great Basin species partition N due to differences in seasonal timing of N uptake. Instead, our results suggest that differences in N capture, and therefore N partitioning, among perennial Great Basin species may be more related to differential species responses to variation in water and P availability, as well as N pulse size, rather than temporal differences in seasonal N uptake between species. Improved soil water availability prior to small N pulses had no effect on N capture by the shrubs, *Chrysothamnus* and *Sarcobatus*, but water addition increased N capture of the grass, *Distichlis*, twofold through the season and tenfold following the June pulse (Fig. 2, upper panels). Soil water status affects a number of soil and plant processes that can influence plant N capture, such as N cycling and supply to roots, root N uptake capacity, and plant N demand. As a result, the differential effect of soil water status on shrub and N capture could be due to several factors. Because N capture by both shrubs did not improve with greater water availability, however, it suggests that the large effect of soil water on *Distichlis* N capture was not a result of increased N availability due to water addition. While we were unable to measure soil water effects on root N uptake capacity in our field study, it is possible that *Distichlis* root N uptake capacity was affected by soil water status more than the shrubs. However, measurements of predawn water potential indicate that *Distichlis* is substantially more drought tolerant than *Chrysothamnus* (J. Richards, unpublished data) suggesting that soil water status effects on *Distichlis* root N uptake capacity alone is unlikely to account for the large (up to tenfold) increase in N capture by *Distichlis* with water addition. The differential effect of water availability on *Distichlis* and shrub N capture is most likely related to the greater rooting depth and access to groundwater by the shrubs compared to *Distichlis*. Low water availability in upper soil layers would not limit shrub N demand but might decrease *Distichlis* N demand later in the growing season. This prediction is consistent with a recent experiment demonstrating that even in late spring and summer when drought is severe, growth of many deep-rooted desert shrubs is not limited by water (Snyder et al. 2004).

In contrast to *Distichlis* and *Sarcobatus*, *Chrysothamnus* N capture from small N pulses increased with greater soil P availability, particularly later in the growing season (Fig. 2, upper panel). Following the small June pulse, P addition increased *Chrysothamnus* N capture threefold relative to plants only receiving water and the amount of N captured was comparable to that in early spring. This suggests that the limited effect of water on *Chrysothamnus* N capture was not due to low soil N supply to roots or because roots were unable to maintain N uptake capacity but was instead due to low soil P limiting plant N demand. Although soil water status may influence P solubility and availability in arid systems, we only observed a significant increase in *Chrysothamnus* leaf P with P addition (Fig. 3) suggesting soil P supply rates were inadequate to meet that species' P requirements. This strong effect of low soil P availability on *Chrysothamnus* N capture is consistent with studies showing that *Chrysothamnus* has a very high leaf P requirement (>5 g kg^{-1}), but a poor ability to recycle and store P (Drenovsky 2002) and also could explain why previous studies have shown that *Chrysothamnus* has a limited ability to respond to N pulses (Bilbrough and Caldwell 1997; Yoder and Caldwell 2002).

Unlike *Chrysothamnus* and *Distichlis*, *Sarcobatus* N capture from small pulses continued to decline through the season regardless of soil water and P availability (Fig. 2, upper panels). Averaged across all treatments, *Sarcobatus* N capture from small pulses was twofold and threefold lower than *Distichlis* and *Chrysothamnus*, with the majority of *Sarcobatus* N uptake restricted to the early spring pulse when soil N concentrations were relatively high. In contrast, *Sarcobatus* N capture from large pulses

was fourfold and threefold greater than *Chrysothamnus* and *Distichlis* across the treatments. Although *Sarcobatus* N capture from large pulses was affected by the timing of the pulse in relation to growth rate, the observation that, within each pulse period, *Sarcobatus* captured the least amount of N from small pulses, but the greatest amount of N from large pulses strongly suggests that the major limitation to *Sarcobatus* N capture from small pulses was soil N availability. When soil N availability increased during large pulses, *Sarcobatus* leaf N increased 60% (Fig. 3), suggesting that the majority of N acquired during the pulse was not used to support additional growth, but was instead stored. Although large pulses may be infrequent in the Great Basin, when they do occur rapid uptake and storage of N by *Sarcobatus* may minimize the impact of subsequent years with low N availability (Aerts and Chapin 2000).

The observation that *Sarcobatus*, the species most tolerant to low water and nutrient conditions, captured less N from small pulses, but more N from large pulses relative to the less stress tolerant species contrasts with our initial prediction and is inconsistent with theory and other experimental reports. Optimality theory predicts a trade-off between root growth rate and root life span (Grime 1994). Less stress tolerant species are expected to capture nutrients more efficiently from large pulses (high in magnitude and long in duration) through rapid growth of relatively short-lived roots. In contrast, more stress tolerant species are expected to capture nutrients from small ephemeral pulses more efficiently through a slow growing, but long-lived, root system. Although empirical support for this theory is limited, we know of no studies that have demonstrated that more stress tolerant species are better able to respond to large nutrient pulses than less stress tolerant species. Nutrient addition, however, has been shown to shift competitive hierarchies in salt marshes, with more stress tolerant plants being more competitive under fertilization but less competitive under ambient nutrient levels (Emery et al. 2001), suggesting more stress tolerant species in that system also are better able to respond to large nutrient pulses. Although our comparisons included only three species, limiting the scope of our conclusions, these observations contrast with predominant theories of competitive ability (Grime 1977; Tilman 1988) and warrant more detailed investigations of potential tradeoffs between stress tolerance and ability to respond to different sizes of nutrient pulses.

While individual species varied in ability to respond to pulses of different size, the plant community as a whole was well adapted to use small N pulses. Recovery of ^{15}N in the vegetation from small N pulses averaged 60% and increased up to 75% with water addition (Table 2). Although microbial ^{15}N capture was not quantified, our high recoveries of ^{15}N 20 days after label injection in relation to previous literature reports suggests that this plant community is very capable of competing for small amounts of NO_3^- released during pulses (Kaye and Hart 1997; Hodge et al. 2000). In contrast, the plant community was substantially less efficient in capturing N from large pulses. Although seasonal declines in N capture from large pulses by the community likely were linked to lower plant N demand, even in early spring when plant demand was high only 16% of the labeled N was acquired in the 20-days period. It appeared that the major portion of the label remained in the soil NO_3^- pool (Table 3). While this pool may have been more depleted if our labeling period was longer, the upper 30 cm of soil was very dry (1–2% volumetric water content) following the May and June pulse even though we applied a 20-mm precipitation event prior to injecting these large N pulses. This suggests that the community as a whole was unable to completely draw down the available NO_3^- before soil dry-down may have inhibited root N uptake. Concentrations of DON increased twofold following large pulses, suggesting this was a second but smaller sink for our N inputs (Table 3). Although there are several mechanisms for DON generation, fine roots were the major plant sinks for N following both small and large pulses, so DON could have been generated from fine root shedding and subsequent microbial decomposition (Neff et al. 2003). A likely second source could be from direct microbial turnover (Seely and Lajtha 1997). DON produced from these two sources is probably relatively labile and would be quickly degraded during subsequent precipitation events.

In arid ecosystems, the ability to rapidly capture N from brief pulses is expected to influence plant survival, growth, and competitive ability (Goldberg and Novoplansky 1997). In this experiment, we demonstrated that plant N capture from pulses was highly regulated, depending on plant growth rate as well as soil water and P availability. An even more important point ecologically, though, is that variation in soil water and P availability and N pulse size differentially affected the ability of these dominate species to capture N from pulses. As a result, this variation likely plays a major role in determining how N is partitioned among species within these communities. For example, *Distichlis* N capture from small pulses may decrease relatively more than the deep-rooted shrubs during low rainfall years or years, when precipitation events are clustered mainly in early spring, potentially altering competitive interactions between the shrubs and grass. Similarly, while *Chrysothamnus* was able to exploit small N pulses better than *Sarcobatus*, N partitioning and competitive interactions between these shrubs may be mediated by the large spatial variation in P that can occur across Great Basin plant communities. In a similar manner, competitive interactions between *Sarcobatus* and the other species likely would depend on pulse size. Thus, while N availability is generally limiting in arid systems, the potential for variable water and P supply and N pulse size to contribute to niche diversification and alter species interactions is apparent and should be integrated with theories predicting

competitive interactions and species co-existence in pulse-driven systems.

Although we lack species-level root data, it is likely that the effects of variable water and P supply and N pulse size on species N capture will have implications for N retention at the plant community level. For example, given the high rooting density of *Distichlis* and large effect of soil water status on *Distichlis* N capture, it is likely that the large increase in ^{15}N retention by the plant community with water addition was mainly due to increased N retention in shoots and roots by *Distichlis* and not the shrubs (Table 2). Likewise, within the community, *Chrysothamnus* appears to contribute little to N retention following large N pulses relative to *Sarcobatus* and *Distichlis*. Thus, even in this Great Basin community with relatively low perennial diversity, the individual species differ substantially with regards to the specific resource conditions allowing optimal N capture from pulses. These different species responses, however, apparently combine to allow relatively stable N retention by the plant community despite greatly fluctuating resource conditions in these ecosystems.

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